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MULTIVARIATE ANALYSIS OF PLEISTOCENE AND RECENT COYOTES (CANIS LATRANS) FROM CALIFORNIA

BY

EUGENE GILES

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN GEOLOGICAL SCIENCES

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MULTIVARIATE ANALYSIS OF PLEISTOCENE AND RECENT COYOTES (CANIS LATRANS) FROM CALIFORNIA

BY

EUGENE GILES

(A contribution from the University of California Museum of Paleontology)

ABSTRACT

Multivariate analysis of cranial measurements of Rancho La Brea and McKittrick (California Pleistocene) coyotes demonstrates that they form a well-delineated group that should receive at least the subspecific distinction from Recent California coyotes that is usually accorded them (*Canis latrans orcutti*). *C. lepophagus* (Texas Blancan) seems to rate only subspecific distinction within *C. latrans*. Discriminant analysis indicates that *C. petrolei* from Rancho La Brea is dubiously distinguished from *C. latrans orcutti*. The separate species status of *C. andersoni*, also from Rancho La Brea, is questioned.

INTRODUCTION

In paleontological classification the paleontologist is required to make a judicious assessment of the relative values of numerous morphological features of the specimen or specimens he is classifying. As an aid to this evaluation he uses taxonomic principles based on studies of existing forms of life, either his own or those of others. But in applying these principles the paleontologist lacks, to varying degrees, evidence that is available to the taxonomist of living animals and plants. The technique used in this study provides a means of analyzing morphological differences and assessing their significance objectively; at the same time, it can be reconciled with variations in individual growth and, to a lesser degree, with the genetic concepts underlying classification.

If the focal point of zoölogical classification is considered to be the definition of the species with reference to discrete, potentially interbreeding animal populations, the paleontologist must reconcile his morphological groupings with this concept of general zoölogical systematics. Wright (1950) has observed that diagnosis by morphology does not at all indicate abandonment of a genetic basis for the classificatory units. The morphological similarities and differences intimately associated with the underlying genetic system inevitably provide in practice the basis for paleontological classification, with whatever assistance relevant stratigraphy may offer. The difficulty lies in determining the significance of morphological differences.

The degree to which morphological variables may be influenced by genetic, ecological, or other factors is one critical problem. Since such factors do not operate independently or remain the same through time according to any theory of natural selection, the problem is complex. Even if the groups under consideration were geographically stable and not subject to infusions from without, evolutionary convergence and parallelism might interfere with the tracing of lineages by means of the material paleontologists ordinarily use. Differing rates of evolution, possible polyphyly, and confused stratigraphy pose additional difficulties.

Paleontology can with increasing fidelity trace the intricate ramifications of the evolutionary course of many organic groups; many existing hiatuses in the fossil record can be spanned confidently because of their smallness in comparison with the period of time involved. These hiatuses, however, impede the observation of the results of evolutionary mechanisms as shown in animal remains. Simpson (1953) emphasizes the minuteness of the change undergone by the critical unit, the breeding population; the small selection pressure exerted through minor differences in relative fertility; and the very moderate degree to which mutations augment genetic variability, as characteristic features utilized in the synthetic approach. But the chance factors affecting fossil preservation generally lead to small, eclectic, discontinuous samples that demonstrate only gross changes.

There are, however, some unusual fossil accumulations that permit analyses to take into account at least some of the variability characteristic of natural populations. The Rancho La Brea vertebrate fauna provides one of the best available series of mammalian fossils. Among the different groups of mammals found in these tar-impregnated deposits are certain canids whose taxonomic assignment has been somewhat difficult. Coyotelike dogs are given special attention in this paper. The abundant wolflike forms, which have previously been subjected to statistical analysis (Nigra and Lance, 1947), and the gray fox will not be considered.

METHOD

Influences from genetic and zoölogical research as well as evaluations of their own material have prompted paleontologists to greater concern for the nature and characteristics of the populations of which their fossil specimens are generally very small samples. This interest can lead to a consideration of possible ways of determining the extent and expression of inter- and intrapopulation variation and the means whereby it may be taken into account. Methods of elucidating the relationships among populations, the units of evolution, are of prime importance. Multivariate analysis provides one mode of attack on these problems.

The biological significance of linear measurements from a specimen with irregular morphology may be open to some question, but it is standard practice to use them in taxonomic studies—either actual dimensions or merely their relative proportions. The measurements taken of the coyotes are of the sort used in such studies. The proposed taxonomic distinctions among the canids considered here have been almost uniformly based on quantitative differences, as is indicated throughout.

P. C. Mahalanobis (e.g., Mahalanobis, Majumdar, and Rao, 1949) has developed a technique by which a number of variables may all be taken into account at the same time when several groups are being analyzed together. Consider a problem involving four closely related groups or populations that are all suspected of differing from one another, yet may not differ from each other to the same degree. If evolutionary significance is placed on differences in over-all morphology, a measure of the degree of difference, or distance, between each population and each of the others would be desirable. Thus, with populations P_1, P_2, P_3, and P_4, some way of reckoning the distances D_{12}, D_{13}, D_{14}, D_{23}, D_{24}, and D_{34} should be sought. These distances, in numbers, might make possible a statement about intergroup relations,

or perhaps show that one or more groups were not definable on the basis of such measurements.

The simplest method would be to choose one character—for example, skull length—which differs among the groups, measure it for all specimens, find the mean for each group, and express the difference among the groups as the difference between each group's mean and the means of the others. This would give numerical values for the symbols D_{12}, D_{13}, and so on. The group whose mean was least like that of another group would thus be placed farthest from it. The modified extension of this method that I have used is not intended to sort out populations from a heterogeneous assemblage. The populations must first be segregated by an external criterion such as location, stratigraphic position, or age.

The complicated morphology of vertebrates suggests that the distance between groups should be determined not just from the differences between the means of one measurement, but from the *sum* of the differences of the means of a theoretically endless series of measurements representing all possible dimensions of the animal. This is not only impossible; it is also unnecessary, for two reasons. (1) Many measurements are practically identical or are merely part of a previously measured dimension, and thus highly correlated with each other, so that each additional measurement adds little to the total picture. (2) The attainable sharpness of discrimination between any two groups is limited by intragroup variability.

If the distance between groups is to be determined by the sum of the differences between the means of a number of measurements or variables (no more than eight or nine are generally feasible), two corrections are necessary to make the calculations reliable. First, the disparity between two mean-differences which is due only to a difference in gross size of the characters measured must be removed: a difference of a centimeter between two means for head length, for example, is not likely to be ten times as important as a mean-difference of one millimeter in molar length. Second, the possibility of error resulting from the correlation between two variables must be removed. If, for example, a specimen with a short head is compared with a specimen with a long one, its head will probably also be narrower than that of the second specimen. Part of this difference in head breadth may be related to a difference in the over-all size of the two specimens, but part may be attributable to the fact that the second belongs to a group with distinctive, characteristically broad heads. The part that is correlated with the difference in over-all size must be excluded before the true value of the breadth measurement can be determined.

Making allowance for correlated measurements is important for another reason. As mentioned earlier, successive measurements tend to become more and more closely correlated, and may finally completely overlap each other. If correlation is not taken into account, the mean-differences of several measurements whose correlation may be as much as 100 per cent will be added to the total sum. This difficulty can be avoided only if the mean-difference added by each new measurement is adjusted in proportion to its correlation with all the measurements coming before it.

Multivariate analysis may also be applied to the problem of allocating a specimen to either of two groups, or possibly excluding it from both. The procedure has two parts: (1) determining whether the specimen could belong to group A, and

also whether it could belong to group B; and (2) if it could belong to either, then determining the one in which it should be placed, i.e., finding a discriminant function by which the specimen may be categorized. Utilization of many measurements and adjustment for correlation are desirable here also.

The technique employed in Mahalanobis's D^2 and discriminant analyses can be visualized roughly by extension from bivariate analysis. If two measurements are taken on each tooth of a series, the results can be plotted as a series of points on an ordinary (Cartesian) graph, with the breadth, say, being plotted on the ordinate, the length on the abscissa. Thus each tooth is represented by a point on the graph. An additional dimension—for example, crown height—would require a three-dimensional, "solid" graph, but each tooth could still be represented by a single point. If a total of n measurements were taken, an n-dimensional space would be required to represent each tooth as a point. It would be desirable to have the points in the cluster that represents a series of teeth so arranged that equal densities of points would form concentric spheres around the centroid. If measurements unadjusted for correlation and disparity in gross size were used, the cluster would be ellipsoid. But by removing mutual correlation and by putting the measurements in standard form (making the mean-differences comparable) the spheroid shape would be attained. If similar operations were performed on measurements of other series of teeth and these all placed in the same n-dimensional space, the amount of separation between the clusters of points representing teeth would be directly related to the distance between their centroids, and further, measurements of any questionable specimen, placed in this n-dimensional space, would assume a position indicating its affinities with the various clusters.

The multivariate technique used in this study demands that the data meet three requirements: (1) that the frequency distribution of the measurements of each variable approximates a normal curve, (2) that the intercharacter correlation is linear, and (3) that the joint distribution of the variables approximates a multivariate normal distribution (Mahalanobis, Majumdar, and Rao, 1949: 120–121, 137–138). If the first two requirements are fulfilled by the data, the probability that the data also fulfill the third is likely but not proved, since the first two requirements are necessary but not the only determinants for the third. No single test is available to demonstrate that the third requirement has been met, but the previous experience of many biologists using morphological data supports the assumption of a normal distribution for the separate variables.

Mixing the sexes could upset the normal distribution expected for measurements taken on material of one sex. A bimodal distribution might be predicted, but it has not been found for the canid measurements. Hildebrand's (1951) data, and data gathered for this study, indicate that canid males average only 3 to 5 per cent larger than comparable females of the same species. The potential bimodality seems to be subsumed in general morphological variability.

The length of the maxillary tooth row in *Canis latrans ochropus* was tested for a normal distribution by the *chi*-square test. The low value obtained indicated a reasonably good fit to a normal curve. In addition to this test, several other variables were plotted on normal-curve graph paper; all described fairly straight lines, as normally distributed data will.

Testing for the linearity of correlation is a real problem. It is often assumed that morphological data of the sort used here are linearly correlated, since many statistical techniques so require. However, it is also widely accepted that when a reasonable size difference is involved, the distribution of the data may be more closely approximated by the allometric formula, $y = bx^k$, which takes differential growth rates into account. This dilemma can be resolved in two ways. The data may be put in logarithmic form (e.g., Burma, 1948), making the allometric formula, $\log y = \log b - k \log x$, a form suitable for linear analysis. Olson and Miller (1951), fully recognizing the importance of allometry, applied various tests that showed it to be insignificant in their material. In an earlier study of my own, mammalian material that was measured in a way similar to that I have used in this study and subjected to other and possibly more sensitive statistical tests of significance than used by Olson and Miller, indicated an allometric rather than a linear distribution of measurements for a majority of dimensions (Giles, 1956*a*). In the present study the probable allometric trend of the data has been ignored and the correlation treated as linear. Testing for allometry would be a study in itself. The deviation, in any case, would be relatively small and unlikely to affect the tests materially (e.g., Mahalanobis, Majumdar, and Rao, 1949).

In addition, random samples are necessary for this sort of statistical technique. Every effort was made to exclude bias in choosing the specimens for measurement; unfortunately, the analyst's possible bias may add to a bias created by the original act of entrapment itself, but I have no reason to suspect that a relevant nonrandom selection pressure operated to provide the samples utilized. Since the D^2 technique is not suited for handling fragmentary data, measurements were restricted to specimens providing the full series.

MATERIAL

The Recent coyote, a mammal of western and central North America, has been placed in one species, *Canis latrans* Say, by current authorities (e.g., Nelson, 1932; Grinnell, 1933; Young and Jackson, 1951). The coyote is readily distinguished from all other canids in its range except the widespread gray wolf (*C. lupus* Linnaeus) and the red wolf (*C. niger* Bartram). The gray wolf greatly exceeds the coyote in size, as well as differing in many details. The red wolf, which is restricted to southeastern United States, is generally larger than the coyote, but some individuals are practically indistinguishable from coyotes where their ranges overlap in eastern Texas (Young and Goldman, 1944).

Jackson (Young and Jackson, 1951) recognizes 19 geographic subspecies of the coyote in his recent revision based on 4,500 specimens obtained during predator control campaigns. Four subspecies occur in California (fig. 1). Grinnell (1933) did not feel justified in distinguishing *Canis latrans clepticus* Elliot as a separate subspecies, but he recognized the other three subspecies. In California, *C. l. clepticus* is found only in the southern part of San Diego County. Demarcation of the four subspecies in all but insular groups is arbitrary; intergradation occurs at the boundaries.

California subspecies recognized by Jackson (Young and Jackson, 1951) and in this paper are: *Canis latrans ochropus* Eschscholtz, the California Valley Coyote,

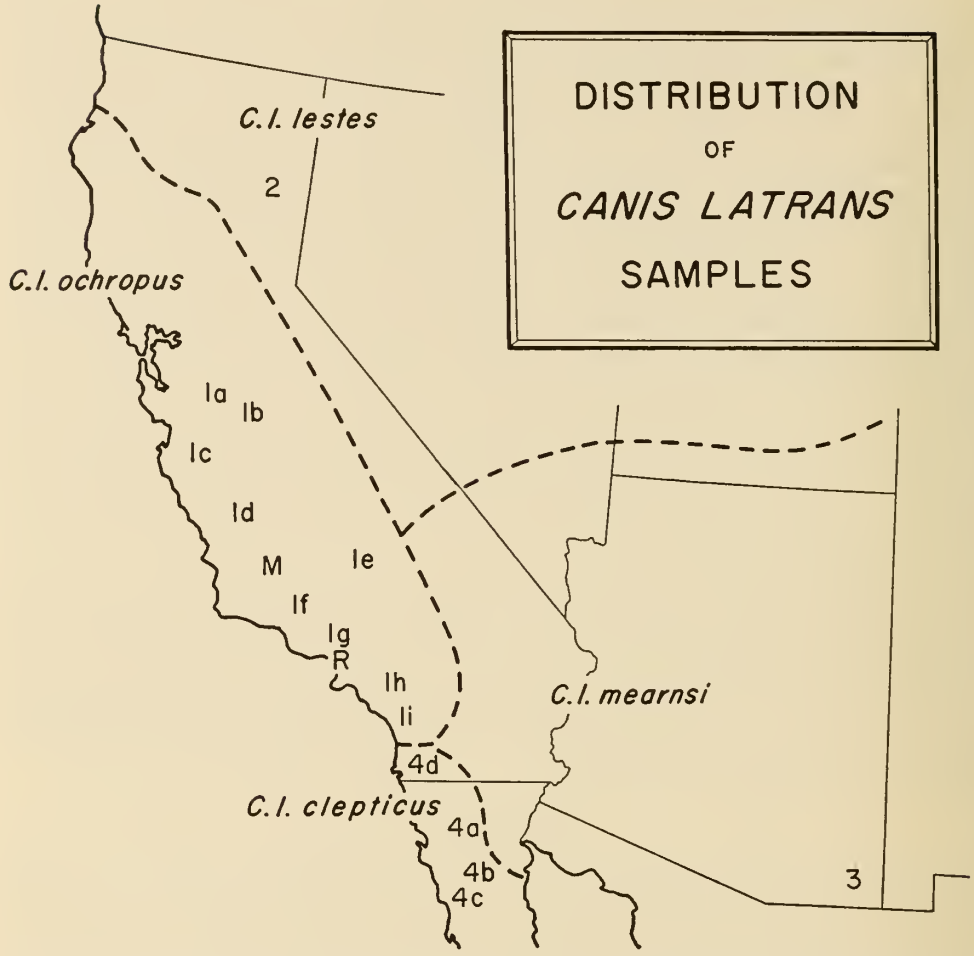

Fig. 1. Geographic origin of coyote samples, by county or region for Recent subspecies studied in this paper. Numbers of specimens in parentheses. *Canis latrans ochropus: 1a,* Stanislaus (1); *1b,* Merced (2); *1c,* San Benito (20); *1d,* Monterey (9); *1e,* Kern (7); *1f,* Ventura (2); *1g,* Los Angeles (3); *1h,* Riverside (5); *1i,* San Diego (1). *C. l. lestes: 2,* Lassen (50). *C. l. mearnsi: 3,* Cochise (50). *C. l. clepticus: 4a,* Sierra Juarez, Baja California (2); *4b,* Sierra de San Pedro Mártir, Baja California (8); *4c,* San Telmo, Baja California (2); *4d,* San Diego (4). *C. l. orcutti: R,* Rancho La Brea (37); *M,* McKittrick (7). Recent subspecies ranges based on Jackson (Young and Jackson, 1951).

ranging in the region west of the Sierras; *C. l. mearnsi* C. H. Merriam (= *C. l. estor* C. H. Merriam), the so-called Mearns or Desert Coyote, ranging in the southeastern part of the state; *C. l. lestes* C. H. Merriam, the Mountain Coyote, ranging in the northeastern section of the state; and *C. l. clepticus* Elliot, the San Pedro Mártir Coyote, a northern Baja California form ranging into San Diego County.

The California Valley Coyote is a medium-sized, dark animal with an elongate skull. The Mountain Coyote is rather large, quite dark, and with a broader skull. The Desert Coyote is the smallest of the California subspecies; it has a bright coat

and a small, weak skull. The San Pedro Mártir Coyote is medium-sized, broad-skulled, and has a predominantly dark or reddish coat.

Jackson (Young and Jackson, 1951) lists certain cranial characters that he considers indicative of the various subspecies (table 1). This table presents a good case for the use of multivariate analysis: it is clear that assessing by eye the rela-

TABLE 1

SOME CRANIAL CHARACTERISTICS OF COYOTE SUBSPECIES

Character	*C. l. ochropus*	*C. l. mearnsi*	*C. l. lestes*	*C. l. clepticus*	*C. l. orcutti*
Frontal region	Nearly flat	Depressed	Flat	.....	.....
Zygomatic arches	.....	.....	Narrow	.....	Very broad
Rostrum					
Breadth	Narrow	.....	Narrow	Broad	Broad
Length	Long	Short	Long	Short	.....
Skull					
Size	.....	Small	Large	.....	Large
Breadth	Narrow	.....	.....	Broad	Medium
Dentition	Weak	Weak, small	Heavy	Moderate	Heavy

SOURCE: Young and Jackson (1951).

tive merit of all these characters would be difficult. Certainly no single character is sufficient to distinguish any one group.

Grinnell (1933:113) states the following in regard to subspecific differentiation:

> Indeed, the three races which are here recognized are not sharply set off; many specimens are so indeterminable by any character whatsoever that their assignment on any save geographic grounds has proved impossible to me. In other words, not only is there intergradation in the usual subspecific sense, but individual variation is so great (at least in the characters of skulls and teeth) that frequent specimens even from the metropolis of one or another of the races do not fit that race!

The fossil canids from Rancho La Brea, as described by Merriam (1910, 1912) and Stock (1938) can be arranged by size, smallest to largest, as follows: *Urocyon californicus* Mearns, the gray fox; *Canis andersoni* J. C. Merriam, a small coyote; *C. latrans orcutti,* the coyote; *C. petrolei* Stock, a more wolflike coyote; *C. lupus furlongi* J. C. Merriam, the wolf; *C. milleri* J. C. Merriam, intermediate between *C. l. furlongi* and *C.* (*Aenocyon*) *dirus* Leidy, the dire wolf.

The coyotes from the Rancho La Brea pits were first given specific rank by Merriam (1910) as *Canis orcutti.* Two years later Merriam (1912) reduced the group to the status of a subspecies of the California Valley Coyote: *C. ochropus orcutti.* Hay (1927) regarded the *orcutti* group as a distinct species, but later workers have considered them to be only a subspecies (e.g., Schultz, 1938). As all Recent coyotes have been placed in one species, *C. ochropus* is a synonym of *C. latrans ochropus.* Thus the Rancho La Brea form will be considered here as *C. l. orcutti.*

The characters by which Merriam (1912) distinguished *Canis latrans orcutti* from other coyotes, especially *C. l. ochropus,* are: somewhat larger skull, broader across the palate and zygomatic arches, higher and thicker mandible, and thicker carnassials.

TABLE 2

MATERIAL USED IN CALCULATIONS

Subspecies	Number of specimens
CRANIUM (BOTH SEXES)	
C. l. ochropus	50
Males	25
Females	25
C. l. mearnsi	44
Males	16
Females	16
Unsexed	12
C. l. lestes	42
Males	19
Females	19
Unsexed	4
C. l. clepticus (San Diego)	4
Males	2
Females	2
C. l. clepticus (Baja California)	12
Males	6
Females	6
C. l. orcutti	
Unsexed	36
CRANIUM (MALES ONLY)	
C. l. ochropus	25
C. l. mearnsi	21
C. l. lestes	23
MANDIBLE	
C. l. ochropus	50
Males	25
Females	25
C. l. mearnsi	50
Males	20
Females	20
Unsexed	10
C. l. lestes	50
Males	25
Females	25
C. l. orcutti (Rancho La Brea)	
Unsexed	37
C. l. orcutti (McKittrick)	
Unsexed	7
C. lepophagus	
Unsexed	6
C. lupus ssp.	
Both sexes	17

Seven coyote mandibles from the tar seeps at McKittrick, California, were measured in addition to the main groups studied for this paper. Schultz (1938) assigned these coyotes to *Canis latrans orcutti*, the subspecies found at Rancho La Brea, and, like other authors, commented on the great variability apparent in a coyote population. The contents of this trap, like those of the Los Angeles pits, have been referred to the Late Pleistocene, with the possibility that those of McKittrick are slightly younger. Some small ecological difference may have existed between McKittrick and Rancho La Brea, which is 110 miles to the southeast, but this difference probably had no effects on the free-ranging coyote.

Six mandibles of coyotelike canids from Randall County, Texas, were also measured. These animals, described by Johnston (1938) as a distinct species, *Canis lepophagus* Johnston, came from beds assigned Blancan age. Johnston's diagnosis of the species states that the *C. lepophagus* cranium is more slender, has stronger crests and postorbital processes, stronger lower jaws, relatively longer teeth, and is generally somewhat smaller than that of *C. latrans*. Although the canid remains occur in two beds separated by a 10-foot stratum lacking mammal remains, evidence indicates that the fauna is localized and represents no great time interval (Johnston and Savage, 1955).

Table 2 lists the specimens studied. Eighty-six per cent of the Rancho La Brea specimens are from the Los Angeles County Museum, the rest from the University of California Museum of Paleontology. The McKittrick specimens are from the Vertebrate Paleontology Collection of the California Institute of Technology (now in the Los Angeles County Museum), the Texas canids from the University of California Museum of Paleontology, and the Recent specimens from the University of California Museum of Vertebrate Zoölogy.

SAMPLING CONSIDERATIONS

The Recent coyote specimens were chosen to represent the smallest possible separation in time and space. The *Canis latrans mearnsi* sample was the most restricted geographically: all the specimens used were collected in Cochise County, Arizona, most of them from the southeastern part of the county, and were acquired over a span of thirteen years (1919–1932). *C. l. lestes* specimens were collected in 1916 in Lassen County, California. Unfortunately, the available specimens of *C. l. ochropus* have been taken over a fairly wide area and in the course of about thirty-five years (fig. 1).

Grinnell (1933) suggested that the great variation among coyotes may arise partly as an artifact of museum collections: a collection built up over time, even though from the same locality, may represent two populations, or even two subspecies—one having moved in rapidly after the first was exterminated. Jackson (Young and Jackson, 1951), however, discounts this argument, but samples for my study were chosen to minimize this possibility.

It is very likely that the specimens of *Canis latrans mearnsi* and *C. l. lestes* are samples of distinct, potentially interbreeding aggregates. The time and geographical spread of the sample of *C. l. ochropus* makes this supposition less probable for it.

The nature of the group taken here as "Rancho La Brea Coyotes" is much less

clear than that of the Recent assemblages. The Rancho La Brea fauna is derived from a single locality well within the geographic range of the modern *Canis latrans ochropus*. Fossil evidence from Rancho La Brea, both plant and animal, corroborates a Late Pleistocene date, not only because of the large number of Recent species and genera present but also by correlation with other deposits known to be of Late Pleistocene origin (Gale, 1932; Schultz, 1938; Grant and Sheppard, 1939; Bailey, 1943; Stock, 1953; Durham, Jahns, and Savage, 1954).

Stock (1953:15) states that the period during which entrapment took place was "a relatively restricted time interval within this [Pleistocene] epoch." Hay (1926) reports that estimates as short as 2,000 years have been made, though he considers a much longer period more reasonable. The small variation in contents among pits, which may or may not be statistically significant, may indicate a valid facies difference. If so, such a difference would indicate a lengthy period of accumulation, which might invalidate consideration of all the coyotes as one sample. A change in environment would not necessarily be reflected in the taxonomy; modern subspecies range through many environmental zones.

Faunal associations of the single find of human remains (pit 10) clearly indicate an entrapment much later than that of the other pits. Although pit 10 is separate from the rest, it is possible that in the other deposits a few Recent specimens might overlie the Pleistocene material, or be mixed in by the movement of the tar. Generally, the likelihood of contamination has not been considered great (Stock, 1953). Here the Rancho La Brea canids have been considered a homogeneous Late Pleistocene population representing a short period of time.

In all cases, only adults, as evinced by permanent dentition, were accepted for study: only males were used for comparisons of Recent subspecies, but both sexes were measured for the more general comparisons with the fossil material. Very large coyote samples taken by government hunters indicate that the sexes maintain a 50 : 50 ratio in the wild state (Young and Jackson, 1951). A similar ratio is assumed for the Rancho La Brea specimens. In some samples the number of Recent males used was limited by the number of females available. To provide a larger sample, equal numbers of known males and females were augmented by unsexed specimens when these were available and satisfied requirements of time and location.

A limitation had to be set on the number of unsexed specimens used, since they might not be half males and half females, and would thus upset the sex ratio in the known-sex group to which they were added—in the extreme case all unsexed specimens might be of one sex. The variation expected when drawing a random sample from a population in which both sexes are equally represented can be calculated from the mean and standard deviation of the binomial distribution. For example, using the normal-curve approximation to the binomial distribution: when $N = 50$, the number of one sex may vary from 19 to 31 and still be within 95 per cent confidence limits. In other words, a sample of 50 that contained 19 males and 31 females would not invalidate the null hypothesis that this sample was drawn from a population in which the sexes were equally represented. Fewer than 19 males (or females) would make the probability less than 1 in 20 that the sample came from a group containing equal numbers of males and females. The number of

unsexed specimens added to a group of known composition was kept within the 95 per cent limits, assuming the extreme case that the unknowns were all of one sex. Such a procedure kept all the Recent samples comparable to the samples from Rancho La Brea.

MEASUREMENTS

Following experimentation, and consideration of the observations of Jackson (Young and Jackson, 1951) and Merriam (1912), eight measurements on the cranium were chosen for analysis. The mandibles were examined with two objectives in mind: to utilize measurements that are readily available in most paleontological series, and to perform the analysis on the basis of as few dimensions as possible, thus reducing statistical manipulation. Only five measurements were taken on the lower jaw. The total number of measurements was 3,500.

For uniformity all measurements were taken to .10 mm. It is not presumed, however, that all measurements are significant to this degree. A complete list of measurements and a fuller account of the statistical procedure have been deposited in the Library of the University of California, Berkeley (Giles, 1956*b*).

The following measurements were used:

Palate-occipital condyle length (POc).—From the posterior border of the palate to the most posterior surface of the occipital condyles parallel to the mid-line.

Length of the maxillary tooth row (MxT).—From the premaxillary-maxillary suture on the labial edge of the alveolar border to the posterior edge of the bony tooth row behind M^2.

Least breadth of the rostrum (LBR).—Breadth of rostrum taken at its least dimension, usually between P^1 and P^2.

Bizygomatic breadth (BzB).—Greatest width of the zygomatic arches.

Interorbital breadth (InB).—Least breadth between the orbits anterior to the postorbital processes.

Frontal height, anterior (FHA).—Measured from the surface of the palate to the juncture between the nasal bones and the frontals in the mid-line, and perpendicular to the long axis of the skull.

Frontal height, posterior (FHP).—Measured from the frontoparietal suture (avoiding any sagittal crest) to the ventral surface of the postsphenoid, perpendicular to the long axis of the skull.

Fourth upper premolar length (P^4L).—Length of carnassial blade on the labial side of the tooth, including the cingulum.

First lower molar length (M_1L).—Taken from the anterior edge of the carnassial blade to the cingulum posterior to the hypoconid.

First lower molar breadth (M_1B).—Breadth taken just anterior to the metaconid.

Mandibular tooth row (MnT).—The length of the mandibular tooth row measured from the posterior edge of the M_3 alveolus to the anterior edge of the canine alveolus.

Horizontal-ramus depth (HRD).—Measured from the anterior part of the lateral edge of the M_1 alveolus to the inferior surface of the mandible, perpendicular to the axis of the horizontal ramus.

TABLE 3

SPECIMENS AND MEANS OF SUBSPECIES BY CHARACTER

Specimen	POc	MxT	LBR	BzB	InB	FHA	FHP	P^4L	Number
CRANIUM (BOTH SEXES)									
C. l. ochropus	85.694	82.150	26.794	94.814	30.952	37.628	46.992	19.054	50
C. l. mearnsi	84.771	80.891	27.039	90.757	30.661	37.900	46.886	19.332	44
C. l. lestes	85.517	82.024	27.112	95.362	31.760	38.902	47.817	19.324	42
C. l. clepticus (San Diego)	82.925	79.550	26.975	88.850	27.800	35.825	46.175	19.750	4
C. l. clepticus (Baja Calif.)	85.083	81.533	27.050	95.158	30.725	37.525	48.242	19.658	12
C. l. orcutti (RLB)	90.633	89.236	31.461	106.819	35.636	41.014	50.122	21.136	36
C. andersoni	81.5	79.0	32.5	93.0	31.5	36.5	46.7	20.6	1
CRANIUM (MALES ONLY)									
C. l. ochropus	87.104	82.908	27.112	96.116	31.240	38.372	47.188	19.360	25
C. l. mearnsi	84.961	82.143	27.433	91.791	31.124	38.800	47.671	19.667	21
C. l. lestes	87.478	83.974	27.652	97.296	32.835	39.857	48.283	19.613	23

MANDIBLE

Specimen	M_1L	M_1B	MnT	HRD	HRB	Number
C. l. ochropus	20.928	7.460	92.522	18.370	8.912	50
C. l. mearnsi	21.200	7.350	91.074	17.664	8.724	50
C. l. lestes	21.236	7.518	92.360	18.702	9.236	50
C. l. orcutti (RLB)	23.730	8.551	98.408	21.938	10.997	37
C. l. orcutti (McK)	22.943	8.314	99.529	22.514	11.057	7
C. lepophagus	21.433	8.033	93.117	21.017	9.700	6
C. lupus ssp.	26.865	10.347	111.312	27.635	12.688	17
C. petrolei	22.5	8.3	97.8	24.5	13.2	1

Horizontal-ramus breadth (HRB).—Measured at the same place as the horizontal-ramus depth, and perpendicular to the vertical axis of the horizontal ramus.

STATISTICAL PROCEDURE

The method and theory of calculating the D^2 statistic and the discriminant function as used in this study are fully set forth in Mahalanobis, Majumdar, and Rao (1949), Rao (1948, 1952), Bronowski and Long (1952), and Mukherjee, Rao, and Trevor (1955).

D^2 is better adapted to morphological studies than certain other methods that might be used (e.g., Pearson's Coefficient of Racial Likeness) in that a simple theoretical determination of the distance between groups is possible, only the fraction of a measurement uncorrelated with other measurements is utilized in discrimination, and sample sizes do not affect the calculations.

Although the technique seems complex, it is rather well fitted to computational schemes and practical application. The laboriousness of the calculations depends on the equipment at hand and the number of variables considered. In many cases three or four rather than the eight measurements used in my analysis of the cranium might suffice—in fact, only five measurements of the lower jaw were enough. Whether the results are considered to be worth the time involved will, of course, depend upon the data tested and the analyst's opinion of the value of statistically based conclusions.

D^2 Analysis

If N groups are to be studied, with p characters measured on each individual, the mean for each of the characters is found for each group (table 3) and then put in standard form. The standard deviation for all of the characters and the coefficient of correlation (r) between each character and the others is found for all groups, as shown in table 4.

The next step is making a transformation to a set of uncorrelated variables. The method by which this is done is described in detail in the references. This transformation results in a series of equations into which the standardized mean values for each character are substituted. The D^2 between each group and the others is found by summing the squares of the differences between each of the transformed values.

When reasonably large samples are used, a *chi*-square test of significance can be applied, using p degrees of freedom (Mahalanobis, Majumdar, and Rao, 1949). The distances between groups can be shown by representing the D values in a diagram. With more than three groups, however, this representation is only approximate.

Discriminant-function Analysis

Burma (1949) used multivariate analysis to test the significance of differences in two invertebrate populations, giving the step-by-step procedure. The D^2 analysis and the discriminant function described below differ considerably in detail from those used in Burma's application. Burma was interested in testing the significance of differences between two groups; my application of the D^2 method defines the relative affinities of a number of groups geographically as well as giving a sig-

nificance test, and the discriminant function is used to place an individual specimen in the proper group.

Often in paleontological work a single specimen will have some features that seem to differ from those of a population of which it is possibly a member: many such specimens seem to be intermediate between two groups. The problem is to determine which of the two groups it came from or whether it came from a third group not before considered. Evidence from the single specimen alone can determine to which group it belongs.

TABLE 4

POOLED ESTIMATES OF CORRELATION COEFFICIENTS AND STANDARD DEVIATIONS

CRANIUM

Character	POc	MxT	LBR	BzB	InB	FHA	FHP	P^4L
POc	.....	.8421	.6726	.7678	.6131	.6296	.5287	.6726
MxT		.....	.7707	.8198	.7232	.6571	.5796	.7787
LBR			.....	.7604	.7006	.6116	.6980	.6779
BzB				.....	.8088	.6707	.7063	.6890
InB					.....	.6753	.6569	.5636
FHA						.....	.5696	.5933
FHP							.....	.5652
P^4L								.....
S.D.	4.500	4.723	2.592	7.583	2.987	2.725	2.203	1.343

MANDIBLE

Character	M_1L	M_1B	MnT	HRD	HRB
M_1L	.....	.8554	.7799	.6628	.7199
M_1B		.....	.7647	.7031	.7414
MnT			.....	.7755	.6777
HRD				.....	.7901
HRB					.....
S.D.	1.546	0.649	4.681	2.166	1.079

The method applied here is a variant of the D^2 analysis discussed above and fulfills the same logical requirements. Because a different set of coefficients is needed, an altered procedure is used to obtain the uncorrelated variables.

A variance-covariance matrix, analogous to the coefficient of correlation matrix referred to in the description of D^2 analysis, is set up. The values should preferably come from the samples under consideration, but a set based on a closely related group will suffice. The samples are assumed to have equal variance-covariance matrices. A unit matrix is appended to the variance-covariance matrix to obtain the uncorrelated factors and the combination is transformed by the pivotal condensation method (Rao, 1952).

To test a single specimen, the values for the number (p) of characters used to describe the specimen are substituted into the linear equation derived from the matrix. This is also done with the mean values of the same characters for the two

groups to which the specimen might belong (table 3). The differences between the results for the single specimen and those for one of the groups are squared and summed. If this sum is not significant at the 5 per cent level when entered in a *chi*-square table, the single specimen might belong to this group. If the same procedure with the other group indicates that the single specimen might belong to it also, a discriminant function must be set up. The value midway between those of the two groups is used in a new linear equation derived from the groups, presuming them to represent populations of the same size. The value for the specimen will fall on one side or the other of this value when substituted into the equation, indicating the specimen's affinities.

DISCUSSION

The possibility of varying rates of evolution always makes the amount of morphological difference an uncertain indicator of evolutionary divergence, which is the basis for classification. Yet since the coyote remains examined in this study represent a very short span of geologic time and since stratigraphy offers no particular aid in pinpointing their evolutionary divergence, to draw inferences from morphological differences is both plausible and necessary. The possibility that similarities may be the result of evolutionary convergence from a polyphyletic origin is present in every taxonomic analysis, but the coyotes arouse no suspicion that this is true of them.

Stirton (1955:28) has modified Mayr, Linsley, and Usinger's (1953) definition of subspecies to include paleontological specimens: subspecies are "geographically and/or stratigraphically defined aggregates of local populations which differ morphologically from other such subdivisions of a species." The question arises, of course, as to the amount of separation necessary in this purely morphological scheme to justify specific or higher ranking. There is no valid reason to consider a statistical difference between two groups as taxonomic per se. The boundaries of the species may be the most objective in taxonomy, but they are by no means unequivocal even in neozoölogical systematics, where the number of characters and the number of specimens from which the inference is made are usually much greater than in paleontology.

Rollins (1953) has suggested that the pertinence of possible collocations be judged by reference to well-defined units within the group under consideration; in other words, by use of what he calls a "species standard." When available, such a standard seems preferable to a procedure that rather inflexibly assigns subspecific rank to groups having characters that overlap and specific rank to those that do not. Mayr (1942:172) has observed that the lower taxonomic groupings grade almost insensibly into those above and below. Stirton (1955) has demonstrated that the often-used criterion of tooth-row length is not sufficient to distinguish established species of the white-footed deer mouse *Peromyscus* because there is overlap among species. Colbert and Hooijer (1953) utilized a species-standard approach in classifying fossil remains of the bamboo rat *Rhyzomys* from China.

Recent coyotes can be used as a "subspecies standard" in guiding taxonomic assignment of fossil specimens. The morphological distance between fossil forms

that is measured by the D^2 analysis can be tied in with definite, accepted neozoölogical subspecific classification because the distance between modern subspecies has been calculated on the same basis. When the distances seems to be of the same general magnitude as among Recent subspecies, the same taxonomic ranking should be applied. The magnitude of interspecific differences is apparent in the comparisons between *Canis petrolei* and *C. lupus* and *C. petrolei* and *C. latrans orcutti*.

D^2 Analysis

In table 5 the D^2 values for the various groups have been listed in order of decreasing magnitude. The greater the D^2 value, the less the affinity between the two groups. Figures 2 to 4 show approximate relationships. The differences are all

TABLE 5

Values of D^2 Arranged in Increasing Order of Magnitude

(Abbreviations: oc = *C. l. ochropus*; me = *C. l. mearnsi*; le = *C. l. lestes*; o_b = *C. l. orcutti* (RLB); o_m = *C. l. orcutti* (McK); lp = *C. lepophagus*.)

C. l. ochropus	*C. l. mearnsi*	*C. l. lestes*	*C. l. orcutti* (RLB)	*C. l. orcutti* (McK)	*C. lepophagus*
		CRANIUM (BOTH SEXES)			
o_b 3.804	o_b 5.119	o_b 3.492	me 5.119		
me 1.627	oc 1.627	me 1.176	oc 3.804		
le 0.634[a]	le 1.176	oc 0.634[a]	le 3.492		
		CRANIUM (MALES ONLY)			
me 4.277	oc 4.277	me 2.709			
le 1.298[b]	le 2.709	oc 1.298[b]			
		MANDIBLE			
o_b 4.502	o_m 6.423	lp 3.828	me 4.863	me 6.423	me 5.981
o_m 4.449	lp 5.981	o_m 3.636	lp 4.581	lp 4.946	o_m 4.946
lp 4.191	o_b 4.863	o_b 3.214	oc 4.502	oc 4.449	o_b 4.581
me 0.743	oc 0.743	me 0.559[c]	le 3.214	le 3.636	oc 4.191
le 0.268	le 0.559[a]	oc 0.268[a]	o_m 1.520[a]	o_b 1.520[a]	le 3.828

[a] Not significant at .05 level. [b] Significant at .05 level. [c] Significant at .02 level.

significant by the *chi*-square test at the 1 per cent level except as noted in the table. The correction factor for small samples has not been applied to the few dimensions that might require it, as it is not likely to affect the results perceptibly.

In the mandible analysis, the two groups of *Canis latrans orcutti*, one from Rancho La Brea and the other from the McKittrick tar seeps, exhibit the phenomenon called "clustering" by Rao (1952). Although this is in no way a precise term, it can be observed that in all but one of the columns containing both groups they fall together, indicating a strong resemblance. When the two are tested against each other, the difference is not significant, and is the lowest in the column.

It is quite clear that these two groups form a single, well-delimited statistical population; it seems equally clear that no taxonomic distinction should be made between them. This evidence parallels the final conclusions reached by Schultz (1938) after a study of the skeleton of the animals from McKittrick.

The Rancho La Brea Coyote evinces a greater similarity to the Mountain Coyote, *Canis latrans lestes*, a northern form, than it does to the coyote, *C. l. ochropus*, living in the Rancho La Brea region today. Although the similarity of *C. l. orcutti* to the Mountain Coyote may suggest changing climate, it should be borne in mind that the distinction between California Valley and Mountain coyotes is slight.

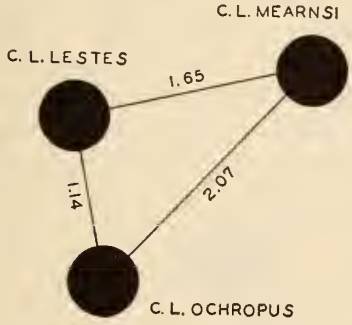

Fig. 2. Approximate *D* distance for three Recent coyote subspecies, based on male crania.

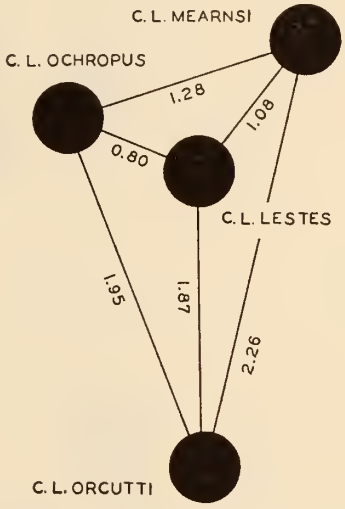

Fig. 3. Approximate *D* distance for four coyote subspecies, based on crania of both sexes.

In borderline cases like that of *Canis latrans ochropus* and *C. l. lestes*, the sensitivity of the different samples measured becomes apparent. The test made from crania of males shows a significant difference between *ochropus* and *lestes* at the 5 per cent level. The test made utilizing male and female specimens is almost but not quite significant at the same level. The mandibular test, employing both sexes and only five instead of eight measurements, is not significant.

Table 5 makes clear that the distinction among the Recent coyote subspecies is considerably less than that between *Canis latrans orcutti* and any one of them. Since all three of the Recent subspecies listed there are well-defined and generally accepted, the Rancho La Brea Coyote should clearly be given at least subspecific status.

Canis lepophagus, from Texas Blancan, is represented by so few specimens that conclusions about its taxonomic status must be very tentative. The evidence would suggest, however, that although *C. lepophagus* is not specifically distinct from the coyotes it is quite probably subspecifically distinct from any one of them, and it has greater affinity to the larger of the Recent coyotes than to the California Late Pleistocene variety.

Discriminant-function Analysis

Stock (1938) states that the mandible of *Canis petrolei* is shorter and more massive than that of *C. latrans orcutti,* has greater convexity of the inferior margin of the horizontal ramus, and shows wider and heavier teeth. The type and sole specimen is a complete mandible in the Los Angeles County Museum collection, No. V5203 (table 3). By means of discriminant-function analysis this specimen was compared with the Rancho La Brea coyote mandibles used in the D^2 test and also with a small collection of Recent wolf mandibles.

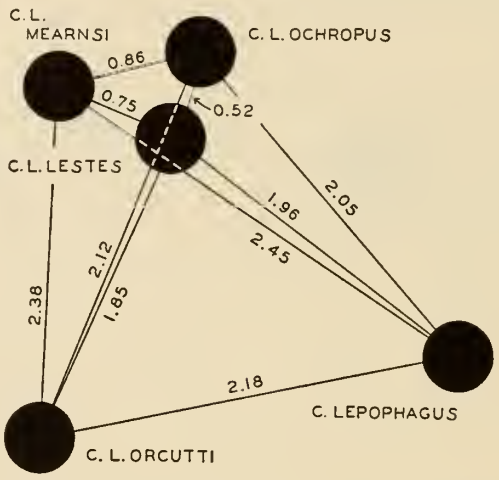

Fig. 4. Approximate D distance for three Recent coyote subspecies, the Rancho La Brea fossil coyote, and *Canis lepophagus* from Texas.

It was considered desirable to compare *Canis petrolei* with rather small wolves and also with wolves of the California area. The earliest modern records indicate that the wolf penetrated but slightly into California and not at all into the Los Angeles region (Young and Goldman, 1944). Of the samples available two subspecies were examined: *C. lupus baileyi* Nelson and Goldman, the Mexican Wolf of the Sierra Madre, which at one time penetrated slightly into southern Arizona, and *C. l. fuscus* Richardson, the Cascade Mountains Wolf, which ranged into northern California. *C. l. fuscus* is a medium-sized wolf; *C. l. baileyi* is the smallest of the North American wolves (Young and Goldman, 1944).

Yates and Healey (1951) warn that discriminant analysis may assign a specimen to one of two groups it is being tested against even though it really does not belong to either. To eliminate this possibility they suggest testing the difference between individual measurements of the specimen and each group. *Canis petrolei* differs significantly from *C. latrans orcutti* only in horizontal-ramus breadth (1 per cent level), but differs significantly from the wolves in first lower molar length and breadth and in mandibular tooth row length (5 per cent level). *C. l. orcutti* and the wolves differ significantly at the 0.1 per cent level in all measurements.

Only horizontal-ramus breadth serves to distinguish *C. petrolei* from *C. l. orcutti.* Following the procedure for discriminant-function analysis, the adjusted mean-differences, summed as for a *chi*-square test, gave these results:

C. petrolei–C. latrans orcutti	15.522
C. petrolei–C. lupus ssp.	32.341

Application of a *chi*-square test shows that this difference between *C. petrolei* and *C. l. orcutti* has a significance very slightly greater than 1 per cent. In other words, a *C. l. orcutti* specimen might be expected to approximate the configuration of *C. petrolei* once in slightly more than a hundred times. Since the levels of significance of the multivariate test and the horizontal-ramus breadth test are both just slightly greater than 1 per cent, there is no morphological patterning characteristic of *petrolei* or *orcutti* as far as the measured dimensions are concerned, except the thicker horizontal ramus in *petrolei.* This, coupled with the extreme divergence of *C. petrolei* from the modern wolf, seems to throw the validity of the species into serious doubt. It should be noted that in 1953 Stock himself expressed some reservations about *C. petrolei*'s status.

Canis andersoni, the small, short-snouted coyote described by Merriam (1910), is represented by the cranium of a single rather young animal, the type (12249) in the collection of the University of California Museum of Paleontology (table 3). Merriam (1912) characterized it as a coyote with a relatively short skull and a short, broad rostrum, and with teeth slightly thicker than average. It has been compared with the *lestes, ochropus, mearnsi,* and *orcutti* coyotes, and in addition has been tested against *C. latrans clepticus,* the coyote of northern Baja California. Twelve specimens of this subspecies were available from Baja California, all collected in the uplands in 1925–1926: four specimens from San Diego County, collected in 1908, provided a separate sample. Jackson (Young and Jackson, 1951) suggested that *C. andersoni* might be closely related to *C. l. clepticus.* Jackson (p. 294) found the skull of *clepticus* "short and broad, with especially rounded cranium and short broad rostrum."

The results of the analysis—given, as before, as summed squared-mean differences—are:

C. andersoni–C. l. orcutti	24.406
C. andersoni–C. l. lestes	28.470
C. andersoni–C. l. ochropus	29.080
C. andersoni–C. l. mearnsi	22.902
C. andersoni–C. l. clepticus (Baja Calif.)	26.941
C. andersoni–C. l. clepticus (San Diego)	17.581

The available specimens do not positively corroborate an *andersoni-clepticus* relationship or suggest another. All except the *clepticus* specimens from San Diego are significantly different from *C. andersoni* at the 1 per cent level. Since the *andersoni* specimen is somewhat juvenile, and thus perhaps not completely diagnostic, it would seem best to withhold judgment on its affinities until more material is available.

Applications and Reliability

The superb preservation of Rancho La Brea material has allowed the application of multivariate analysis to samples large enough to have statistical significance. But often only small samples can be assembled, and it seems reasonable that some sort of multivariate analysis similar to that used in this study could be applied to such samples, with emphasis placed on the descriptive value of the technique. The multivariate test can provide an evaluation of subtle quantitative differences when the interpretation of the differences between single measurements on two or more samples is difficult.

TABLE 6

Percentage Comparisons of Distance (D) by Different Samples

Samples compared	Cranium	Mandible
ochropus–lestes/ochropus–mearnsi	62.5	60.5
ochropus–lestes/mearnsi–lestes	74.1	69.3
mearnsi–lestes/ochropus–mearnsi	84.4	87.2
ochropus–mearnsi/ochropus–orcutti	65.6	40.6
ochropus–mearnsi/mearnsi–orcutti	56.6	36.1
ochropus–lestes/ochropus–orcutti	41.0	24.5
ochropus–lestes/lestes–orcutti	42.8	28.1
ochropus–orcutti/mearnsi–orcutti	86.3	89.1
lestes–orcutti/ochropus–orcutti	95.9	87.3
lestes–mearnsi/mearnsi–orcutti	47.8	31.5
lestes–mearnsi/lestes–orcutti	57.8	40.5
lestes–orcutti/mearnsi–orcutti	82.7	77.7

Fragmentary material creates another problem in paleontological work: the measurements used here for the study of the coyotes might be impossible to obtain from other samples because the material was distorted or incomplete. In studies of such material, measurements of several small but taxonomically important characters might be useful. In table 6 the distance (D) between each group and another (given in figures 3 and 4) has been expressed as a percentage of the distance between one of the pair and a third group. Since the percentages based on the eight-variate cranial analysis are, with only two exceptions, larger than those based on the five-variate mandibular analysis, the cranial analysis has separated the groups to a greater degree. But with the perfect Recent material (the first three entries in table 6), the five mandibular measurements provide a basis for classification that is practically as good as that provided by the eight measurements of the cranium. Imperfections in the Rancho La Brea material result in the five-variate analysis having the same definite trend but not the same absolute magnitude as the eight-variate procedure.

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